CHROMOSOME RACES OF *GRAYIA BRANDEGEI* (CHENOPODIACEAE)

HOWARD C. STUTZ
Department of Botany and Range Science,
Brigham Young University, Provo, UT 84602

STEWART C. SANDERSON and E. DURANT MCARTHUR
Shrub Sciences Laboratory, Intermountain Research Station,
735 North 500 East, Provo, UT 84601

CHU GE-LIN
Institute of Botany, Northwest Teachers College,
Lanchou, Gansu, The People's Republic of China

ABSTRACT

Diploid ($2n = 18$) and tetraploid ($2n = 36$) races of *Grayia brandegei* differ in phenotype and geographic distribution. Diploids have narrow, linear leaves and mostly are restricted to south-central Utah and northeastern Arizona. Tetraploids are larger statured, bear larger, more oval leaves and mostly occur in isolated populations in northeastern Utah, south-central Wyoming, eastern Colorado, and northwestern New Mexico. Because of their morphological and distributional differences, the tetraploid form is designated as a new variety, **Grayia brandegei** var **plummeri**.

Grayia brandegei was described by Asa Gray (1876) from specimens obtained by Brandegee on the banks of the San Juan River in Utah, near the border of Colorado. It differs from the only other species in the genus, *G. spinosa* Moq., in several morphological features and geographic distribution. Whereas *G. spinosa* has a widespread distribution throughout western United States, *G. brandegei* is limited mostly to the drainage of the Colorado River in eastern Utah and adjacent states. Their ranges overlap in several places and appear to be separated primarily by edaphic differences.

Grayia brandegei usually grows on heavy clay soils or sandy loams, but is not restricted to the Chipeta formation, as suggested by Collotzi (1966). Like most other shrubs of the Chenopodiaceae, except *Atriplex,* it lacks Kranz-type leaf anatomy and presumably has the C_3 photosynthetic pathway. Contrary to previous reports, it is monoecious rather than dioecious. Leaves appear in early April, before flowering, and abscise in late summer.

Some populations of *G. brandegei* contain large robust plants with broad, oval leaves, whereas others have smaller-statured plants with narrow, linear leaves. To determine the basis for interpopulational differences, comparative morphological and cytological studies were

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TABLE 1. LOCATIONS OF POPULATIONS OF *Grayia brandegei* EXAMINED FOR CHROMOSOME NUMBER AND MORPHOLOGICAL FEATURES. Soil properties were examined for those populations marked with *.

Diploids	Tetraploids
*AZ, Apache Co., 16 km n. of Many Farms	*CO, Garfield Co., 12 km nw. of Rifle
*CO, Mesa Co., 16 km w. of Mack	NM, San Juan Co., 10 km n. of Aztec
*UT, Grand Co., 8 km nw. of Moab	NM, San Juan Co., 20 km se. of Bloomfield
*UT, San Juan Co., 16 km s. of Blanding	*NM, San Juan Co., 8 km e. of La Plata
UT, San Juan Co., 20 km se. of Hites Crossing	UT, Emery Co., 16 km e. of Fremont Jct.
UT, San Juan Co., 1 km w. of Ismay Trading Post	UT, Garfield Co., 1 km e. of Henrieville
*UT, San Juan Co., 6 km n. of Montezuma Creek	*UT, Kane Co., Cottonwood Wash, 1 km s. of Cannonville
	*UT, Sanpete Co., 10 km nw. of Sterling
	*UT, Uintah Co., 18 km e. of Roosevelt
	UT, Wayne Co., 3 km e. of Notom Exit 24
	UT, Wayne Co., 10 km n. of Baker Ranch, Thousand Lake Mt.
	*WY, Carbon Co., 3 km nw. of Baggs

made on plants that grow in each of 19 populations distributed throughout the range of *G. brandegei.*

METHODS

Chromosome counts were made from microsporocytes in male buds taken from plants in natural populations or from mitotic cells in root tips taken from actively growing seedlings that were germinated on blotter paper in Petri dishes. In each case, the tissues were fixed in aceto-alcohol (1:3, v/v) and stained in aceto-carmine for microscopic examination. Numbers were determined for at least two plants in each of the 19 populations listed in Table 1.

Measurements of plant height and width, and leaf length and width were made on 20 plants in each population. Because the plants are mostly iso-diametric, plant volume was determined by plant height $\times\ \pi(\text{plant diameter}/2)^2$. Plants measured were taken at random at intervals of six feet along a linear transect through each population. Each leaf measured was the largest leaf on a randomly selected twig taken from each plant. Morphological characteristics were compared between ploidy levels using one-way ANOVA (Table 2). Voucher specimens from each population are deposited at Brigham Young University (BRY).

Soil samples were obtained from the site within each population by mixing together five shovelfuls of soil taken at six-foot intervals in a randomly selected linear transect. Cations of the soils were

TABLE 2. MEAN AND STANDARD DEVIATIONS OF PLANT STATURE AND LEAF DIMENSIONS OF DIPLOID (n = 140) AND TETRAPLOID (n = 240) FORMS OF *Grayia brandegei.* Measurements are from 20 plants in each of the populations listed in Table 1. All values significant at $p < 0.0001$ except when indicated.

	$2n$	$4n$	F (df = 378)
Plant ht. (cm)	31.23 ± 10.14	37.03 ± 13.35	19.78
Plant w. (cm)	71.21 ± 28.28	84.46 ± 33.59	15.41
Plant vol. (dm^3)	127.22 ± 97.21	307.66 ± 263.04	13.69
Leaf l. (mm)^{ns}	34.86 ± 10.17	33.87 ± 13.04	0.60
Leaf w. (mm)	3.83 ± 1.47	9.13 ± 5.21	138.62
Leaf l/w ratio	9.59 ± 2.27	4.18 ± 1.67	708.21

analyzed in a Perkin Elmer 5000 Atomic Absorption Spectrophotometer. A saturated water extract was used for the analysis of the macronutrients Ca, Mg, K, and Na. The micronutrients Cu, Fe, Mn, and Zn were extracted in DTPA. P content was determined colorimetrically from a Na_2CO_3 extract. Na absorption ratio (SAR) was calculated from the values obtained for Na, Ca, and Mg. Cation exchange capacity (CEC) was determined by the ammonia distillation method. Texture was determined by the hydrometer method.

RESULTS

Cytological studies showed that plants in the population first collected by Brandegee in southeastern Utah near Ismay Trading Post were diploid with $2n = 18$ chromosomes. Diploid chromosome counts also were obtained from plants in six other populations (Table 1). In each population, the plants had narrow, linear leaves (Fig. 1, Table 2). In 12 other populations of *G. brandegei,* plants were more robust and had considerably wider leaves (Figs. 1, 2, 3, and Table 2). Those individuals examined were found to be tetraploid with $2n = 36$.

Tetraploid populations are more widely distributed than diploid populations (Fig. 3). Putative diploid populations, in which the plants are small-statured and bear narrow, linear leaves, are found along the San Juan River in southeastern Utah. Putative tetraploid populations, in which the plants are larger statured and bear wider leaves, are common in central and northeastern Utah, northwestern New Mexico and northwestern Colorado.

The only known population of *G. brandegei* outside the Colorado River drainage is located west of Sterling, Sanpete County, Utah. This sizeable tetraploid population is growing on Tertiary, Green River clays that are locally abundant, but are otherwise rare in the Great Basin drainage of Utah. This geological formation is common

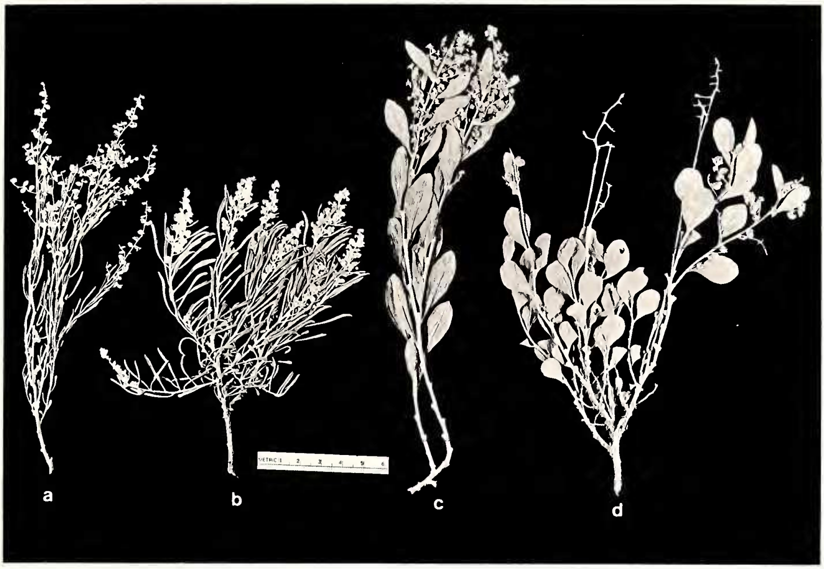

FIG. 1. Twigs of diploid (a, b) and tetraploid (c, d) *Grayia brandegei*. a. AZ, Apache Co., 16 km n. of Many Farms. b. UT, San Juan Co., 6 km n. of Montezuma Creek. c. WY, Carbon Co., 3 km nw. of Baggs. d. UT, Uintah Co., 18 km e. of Roosevelt.

in the northern portion of the Colorado Plateau, and some of the tetraploid populations in eastern Utah and western Colorado occur on it.

All macro- and micronutrients among populations noted in Table 1 showed no significant differences. Similarly pH, CEC, SAR, and soil texture showed no significant differences.

ANOVA for between-population differences for plant height and width and leaf length and width of 12 tetraploid populations were all significant (F-test, $p < 0.0001$).

DISCUSSION

The distribution pattern of diploid and tetraploid populations of *G. brandegei* in Utah, Wyoming, Colorado, Arizona and New Mexico suggests that the tetraploids were derived from the diploids. Because there are no other species that appear to have been involved in their origin, tetraploids are probably autotetraploids. Because of the conspicuous inter-populational differences among them, they probably arose polyphyletically.

Repeated establishment of autotetraploid populations from diploid progenitors could be best explained as originating via triploids. Occasional triploids, arising in a diploid population from fertiliza-

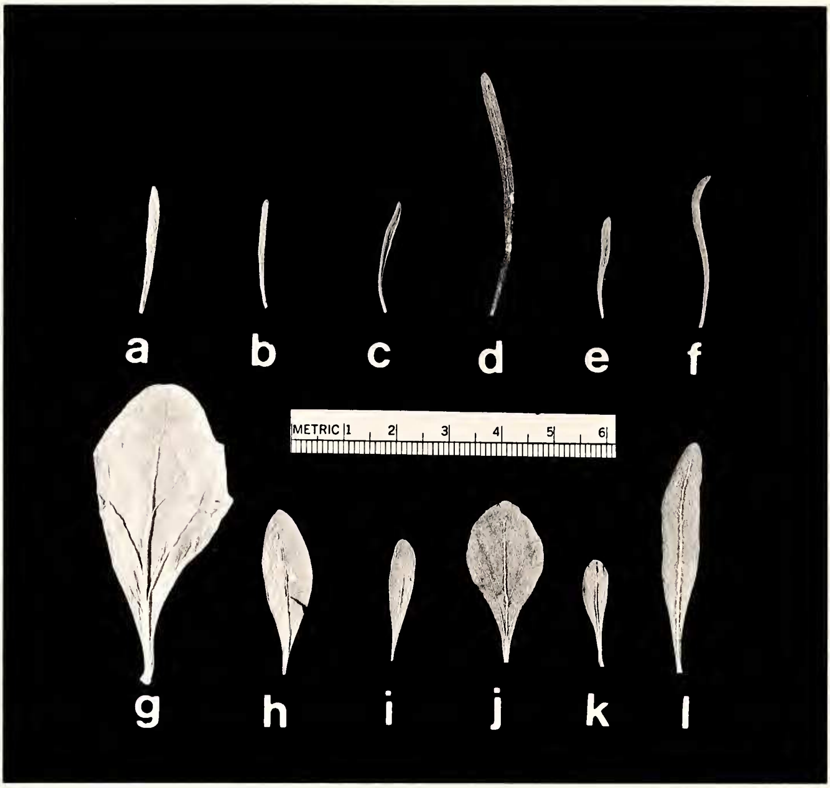

FIG. 2. Leaves of diploid (a–f) and tetraploid (g–l) *Grayia brandegei*. a. UT, Grand Co., 8 km nw. of Moab. b. UT, San Juan Co., 6 km n. of Montezuma Creek. c. UT, San Juan Co., 16 km s. of Blanding. d. CO, Mesa Co., 16 km w. of Mack. e. AZ, Apache Co., 16 km n. of Many Farms. f. UT, San Juan Co., 1 km w. of Ismay Trading Post. g. UT, Uintah Co., 18 km e. of Roosevelt. h. WY, Carbon Co., 3 km nw. of Baggs. i. UT, Sanpete Co., 10 km nw. of Sterling. j. UT, Emery Co., 16 km e. of Fremont Jct. k. CO, Garfield Co., 12 km nw. of Rifle. l. UT, Kane Co., 30 km s. of Cannonville.

tion of unreduced gametes, could generate bursts of additional triploids and tetraploids, because most aneuploid gametes from triploids are expected to fail. Progeny from triploids, therefore, would be diploids, triploids and tetraploids. The diploids would breed normally; the tetraploids would leave only triploid progeny; the triploids would again leave diploids, triploids and tetraploids. Consequently, there could arise, from an occasional triploid, self-accelerating bursts of triploids and tetraploids until sufficient tetraploids occurred to permit autonomous perpetuation.

Tetraploid plants of *G. brandegei* differ from diploids phenotyp-

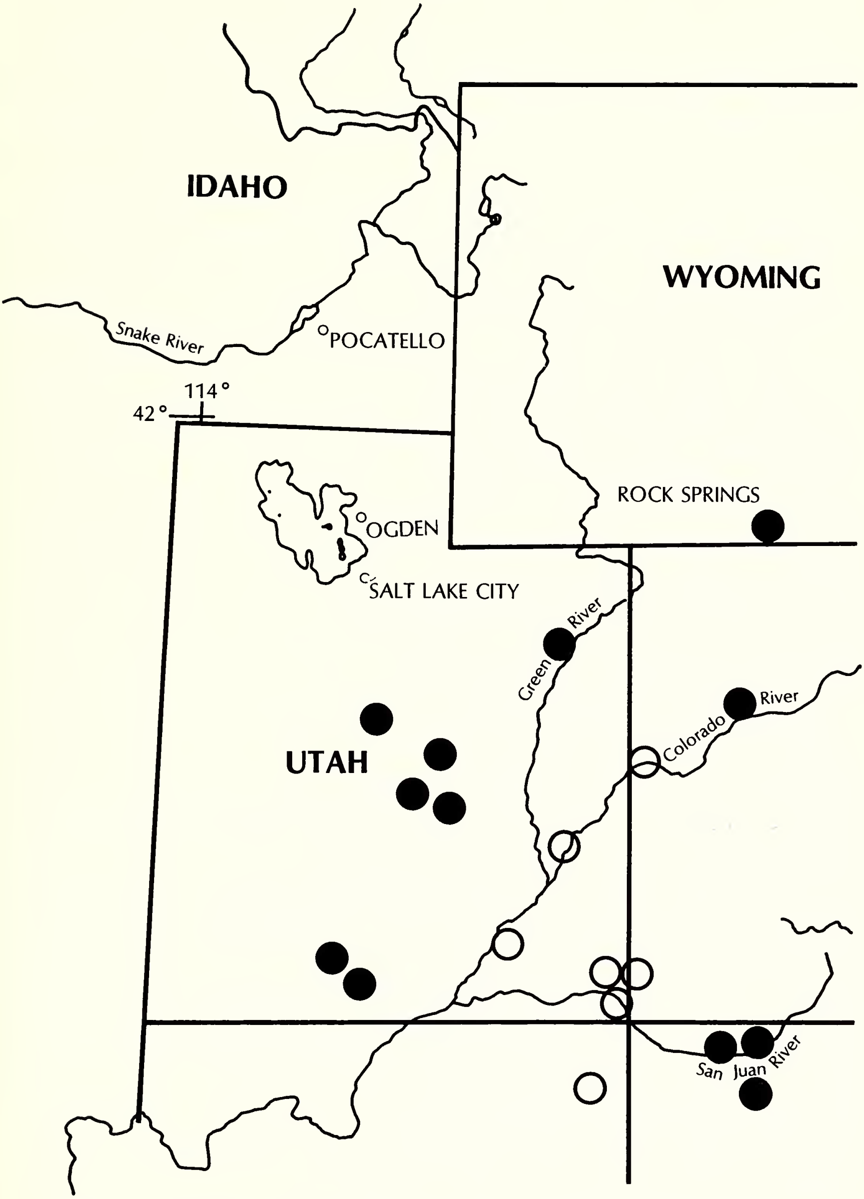

FIG. 3. Distribution of verified diploid and tetraploid forms of *Grayia brandegei*. Symbols: ○ = 2X, ● = 4X.

ically, particularly in stature and leaf-width, and have different geographic distributions, and so we propose them as a distinct variety.

Grayia brandegei A. Gray var. **plummeri** Stutz and Sanderson, var. nov.

Similis var. *brandegei* sed foliis latioribus, plantis altioribus, latioribus et tetraploideis differt, chromosomatum numerus $2n = 36$.

Erect shrub 6–14 dm high, 2.4–6 dm broad; branches erect or ascending, densely and finely pubescent. Leaf blades elliptic, ovate, obovate or oblanceolate, 2.5–6 cm long, 5–22 mm wide, apex obtuse or rounded. Leaf-anatomy non-Kranz. Heterodichogamously monoecious. Male inflorescence glomerulate, the glomerules borne in axils of leaves or small bracts; perianth 4–(5) parted, segments membranaceous, obovate; stamens 4(5), filaments subulate, anthers didymous, included. Female inflorescence paniculate, the flowers borne in axils of leaves or small bracts; bibracteolate, bractlets 5–6 mm wide, orbicular, completely united, margins extended into two wings 4–8 mm broad; perianth lacking; stigmas 2, filiform; utricle orbicular, compressed, included in the two bracts; pericarp membranaceous, free. Seed orbicular, 2–4 mm broad, erect; testa thin, membranaceous; embryo annular; endosperm copious; radicle inferior. Chromosome number: $2n = 36$.

TYPE: USA, UTAH, Duchesne Co.: ca. 18 km e. of Roosevelt, 31 Aug 1984, *Stutz 9325* (Holotype: BRY).

PARATYPES (all deposited in BRY): USA, CO, Garfield Co.: ca. 12 km nw. of Rifle, 18 Aug 1979, *Stutz 8478*. Moffat Co.: Sand Wash near Dugout Draw, T10N R97W S28, 31 Aug 1982, *Parks 908*. Rio Blanco Co.: 25 km e. of Rangely on US 64, 7 Jun 1965, *Collotzi 551*. NM, San Juan Co.: Angel's Peak badlands, ca. 20 km se. of Bloomfield, 5 Jun 1985, *Stutz 9438*. UT, Daggett Co.: East Grindstone Spr., e. end of Antelope Flat, T3N R22E S24, 6600 ft, 29 Aug 1978, *Neese and England 6648*. Emery Co.: I-70, ca. 16 km e. of Fremont Jct., 10 Sep 1983, *Stutz 9153*. Garfield Co.: 1 km e. of Henrieville, 20 Jun 1986, *Stutz 94337*. Kane Co.: Cottonwood Wash, ca. 12 km n. of US hwy 89, 12 Sep 1971, *Atwood and Kaneko 3319*. Sanpete Co.: clay hills w. side antelope valley, 10 km nw. of Sterling, 21 May 1984, *Stutz 9245*. Uintah Co.: ca. 18 km e. of Roosevelt, 25 May 1985, *Stutz 9430*. Wayne Co.: 3 km e. of Notom Exit, Hwy 24, 20 Jun 1984, *Stutz 9374*. WY, Carbon Co.: 3 km nw. of Baggs, 1 Sep 1984, *Stutz 9330*.

The varietal name is chosen to honor A. Perry Plummer who has pioneered numerous important studies of shrubs in western North America. He also discovered the only known population of *Grayia brandegei* growing in the Great Basin (Utah, Sanpete Co., 10 km w. of Sterling, 21 May 1984, *Stutz 9245*).

Acknowledgments

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ANNOUNCEMENT

Graduate Student Awards

The Eleventh Graduate Student Meetings of the California Botanical Society were held Saturday 25 April 1987 at the University of California, Davis. Sixteen papers were presented and awards were presented to the following individuals:

Completed Research

First Place—Jon Hart, UC Davis
Second Place—George Robinson, UC Davis

Research in Progress

First Place—Bruce Baldwin, UC Davis
Second Place—Herb Saylor, San Francisco State University
Third Place—Sam Hammer

Proposed Research

First Place—Stacy Giles, San Francisco State University
Second Place—Barbara Gartner, Stanford University
Third Place—Mike Wood, San Francisco State University

Naill McCarten
Graduate Student Representative